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Reduction in Growth of Pole-Sized Ponderosa Pine Related to a Pandora Moth Outbreak in Central Oregon

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Abstract

A pandora moth (*Coloradia pandora* Blake) outbreak began in 1991 in a ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws) spacing study area that also included scattered sugar pine (*P. lambertiana* Dougl). The relation of defoliation to five tree spacings (with and without understory vegetation) was examined, and stand growth reduction due to defoliation was estimated. Defoliation generally increased as spacing varied from 2 to 5.7 meters and then decreased as spacing increased to 8 meters. Partial defoliation in 1992 reduced stand volume growth, while partial defoliation in 1994 reduced height growth during 1990-94. Basal area growth of nondefoliated sugar pine and partially defoliated ponderosa pine in the outbreak area was compared with basal area growth of nondefoliated ponderosa pine trees outside the outbreak area. Ratios of annual basal area increments for nondefoliated trees to annual increments of partially defoliated ponderosa pine sharply increased after the outbreak. Basal area annual increments of sample trees were reduced by 25 percent in the first growing season after defoliation (1992), 30 percent the second year after defoliation (1993), and 63 percent after the second defoliation (1994).

Keywords: Ponderosa pine, pandora moth, defoliation, growth loss.

Introduction

A pandora moth (*Coloradia pandora* Blake) outbreak was first detected in parts of central Oregon in 1988 (Wickman and others 1996). This insect has a 2-year life cycle (Patterson 1929). Larvae feed on needles of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws) and lodgepole pine (*P. contorta* Dougl. ex. Loud.) on warm winter days and in the spring and early summer of alternate years (even-numbered years in this outbreak). The larvae migrate to the forest floor in early summer and pupate in the soil. Pupae spend a year in the soil, then moths emerge and lay eggs in late June and July (odd-numbered years in this outbreak). Eggs hatch in August and new larvae feed until cold weather begins in late fall. Buds are not damaged, and foliage produced in years of moth flight is little affected. Outbreaks collapse after three or four generations when a naturally occurring virus infects the larvae. Two previous outbreaks have occurred in Oregon in this century.

The outbreak spread to a ponderosa pine spacing study in 1991, and partial defoliation occurred in 1992 and 1994. The spacing study, initiated in 1959 (Barrett 1982), consisted of pole- and small saw-log-sized trees when this outbreak was detected. The last measurement period included the 1990 through 1994 growing seasons. Occasional sugar pine (*P. lambertiana* Dougl.) were scattered throughout the study area between the plots and were not defoliated. Pole- and small saw-log-sized stands of ponderosa pine not affected by the outbreak occurred 11 kilometers west of the spacing study area.

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The outbreak in the spacing study area provided an opportunity to (1) examine the relation of stand density and defoliation; (2) estimate stand growth reduction in the spacing study for 1990-94 due to defoliation in 1992 and 1994; and (3) make implications concerning basal area growth of nondefoliated sugar pine, partially defoliated ponderosa pine, and nondefoliated ponderosa pine before and after 1992 when partial defoliation first occurred. Nondefoliated sugar pine in the spacing study area and the nondefoliated ponderosa pine stands nearby provided data for these implications.

Methods

Study Area

The study area (56 kilometers southwest of Bend, 43° 44' N., 121° 36' W.; 1340 meters elevation) has an average slope of 10 percent and a predominately east-facing aspect. Mean annual precipitation of 61 centimeters falls mainly from October through April and a 60-centimeter snowpack is common between January and March. Understory vegetation is dominated by the shrub species antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), greenleaf manzanita (*Arctostaphylos patula* Green), and snowbrush (*Ceanothus velutinus* Dougl. ex Hook). Scattered Ross sedge (*Carex rossi* Boott), western needle grass (*Stipa occidentalis* Thrub. ex Wats.), and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith) are present.

The soil, a Xeric vitricryand, is developing on 84 centimeters of dacite pumice from the eruption of Mount Mazama (now Crater Lake). The surface texture is loamy coarse sand.

Spacing Study Treatments and Design

The old-growth ponderosa pine overstory was removed and the remaining suppressed understory trees were thinned in 1958-59. Thirty 0.078-hectare plots were distributed across the 65-hectare thinned area. Each 24.1- by 32.2-meter plot was surrounded by a similarly treated 10-meter buffer strip. Six replications of five tree spacings were randomly assigned: 2.0 meters (2,469 trees hectare^{-1} [TPH]), 2.8 meters (1,235 TPH), 4.0 meters (617 TPH), 5.7 meters (309 TPH), and 8.0 meters (154 TPH). All understory vegetation was removed in spring 1960 and at successive 3- to 4-year intervals on three randomly chosen plots per spacing and allowed to develop naturally on the three remaining replications. The design was a completely randomized 5-by-2 factorial with three replications, and became a split-plot in time for variables measured in different periods or years (Barrett 1982).

Spacing Study Measurements and Analyses

Diameters and heights of all plot trees were measured in fall 1959, 1963, 1967, 1971, 1975, 1979, 1984, 1989, and 1994, providing data for five 4-year and three 5-year periods. Tree volumes were calculated by using equations for second-growth ponderosa pine developed by DeMars and Barrett (1987). Periodic annual increments (PAIs) for gross basal area, gross volume, and average height for surviving trees were determined for each of the eight periods. After the 1992 and 1994 partial defoliations, defoliation percentage for each plot was estimated by examining tree crowns with the aid of binoculars. Each plot tree was examined on the two widest spacing treatment plots, and at least 15 trees per plot were examined on the remaining plots. These 15 trees were randomly chosen from different 5-centimeter diameter stem classes. Pandora moth larva leave a small amount of needle next to the fascicle, thereby allowing an estimate of the needle complement present before defoliation. Percentage of plot defoliation was estimated by averaging the values of percentage of defoliation determined for the plot trees.

Analyses of Spacing Study Results

Split-plot analysis of variance (SAS Institute 1988) was used with the plot defoliation data to test the following hypotheses: (1) no differences in defoliation occurred with spacing; (2) defoliation did not differ with understory vegetation treatments; and (3) defoliation was the same in 1992 and 1994.

Growth percentages of gross basal area, average height, and gross volumes for each spacing study plot were calculated as,

$$\text{growth percent} = 100(\text{PAI}/X) ,$$

where PAIs were for 1990-94 and X was the value of basal area, average height, or volume of live trees at the beginning of the period (spring 1990). These growth percentages then were subjected to analyses of variance, with percentage of defoliation in 1992 and 1994 added as covariates to the spacing, understory, and spacing-by-understory variables (SAS Institute 1988). These analyses tested the hypotheses that growth percentages did not differ with percentage of defoliation in 1992 or 1994, spacing, or the presence of understory. Covariance analysis assumes covariates are independent of treatments; otherwise treatment effects can be reduced or removed.

Because there are five spacing treatments, a fourth-degree polynomial can be used to describe the percentage of defoliation-spacing and the percentage of growth-spacing relations. Linear, quadratic, cubic, and quartic effects were tested by using orthogonal polynomial methods (Bliss 1970).

Additional Measurements and Analyses

Increment cores from 17 sugar pine and 23 partially defoliated ponderosa pine growing between spacing plots were taken in late 1994. Increment cores also were taken from 54 nondefoliated ponderosa pine trees. Thirty-one of those nondefoliated trees were in an unthinned stand on flat topography 11.7 kilometers west of the study area near Twin Lakes. The remaining 23 nondefoliated trees were in a thinned stand on a pumice- and ash-mantled lava flow 14 kilometers west and 7° north of the spacing study area. Elevation at both areas was 1340 meters. Selection of these trees was not based on a random sample of all trees present on these sites. Trees were sampled to cover the range of tree sizes present in the stands. For the ponderosa pine in the spacing study area, an additional criteria was a degree of defoliation approximately equivalent to the average defoliation of the spacing study plots. Because of this selection process, implications, but not inferences, can be made from the analyses. Diameters of all sampled trees and bark thickness at breast height for all sampled sugar pine were determined at the time of boring. Polynomial regression methods were used to develop the relation between bark thickness and diameter for sugar pine. Annual increments of radial wood growth were determined for 1985-94. Ring widths were measured to the nearest 0.01 millimeter with an electronic microcaliper linked to a microcomputer. Diameters outside bark were estimated at yearly intervals by using the radial wood increments and the bark thickness equation of DeMars and Barrett (1987) for ponderosa pine or the equation developed from the bark thickness measurements for sugar pine.

Periodic annual basal area increments (PAIs) of the sample trees were determined from the estimated outside bark diameters for 1989-91 and 1992-94 for the four area-species combinations (spacing study area-sugar pine, spacing study area-ponderosa pine, Twin Lakes-ponderosa pine, lava flow-ponderosa pine). These PAIs for the two

periods (3 years before and 3 years after initial pandora moth defoliation in the spacing study area) were subjected to split-plot analyses of variance (SAS Institute 1988). These analyses tested the hypotheses that tree basal area growth rates did not differ with species-area combinations or period.

Assuming the effects of the drought, ongoing since the mid-1970s (Cochran 1998), were the same in all three areas, a procedure was derived to isolate the effect of the pandora moth outbreak from the effect of drought on basal area increment of the sampled trees. Annual basal area increments of individual trees (AI) for the four species-area combinations were adjusted to a common tree basal area at the start of each growing season to begin the procedure. These adjustments were made by performing regression analyses (SAS Institute 1988) for each year (1985 through 1994, i = 1 through 10) by using the model,

$$AI_i = a_i + b_{i,j}(SA_j) + c_i(IBA_i) + d_{i,j}(SA_j)(IBA_i) \ , \qquad (1)$$

where SA_j is an indicator variable (j=1,2,3) representing the four species-area combinations, and IBA is the individual tree basal area at the start of the growing season.

Basal area increments of the bored ponderosa pine ($AIDP_i$) and sugar pine ($AISP_i$) in the spacing study area for 1992 (i = 8), 1993 (i = 9), and 1994 (i = 10) without defoliation then were estimated. This estimation required four steps.

Step 1: Six ratios (k = 1 through 6) of adjusted means of annual increments were determined for each growing season (i = 1 through 10) during 1985-94:

Annual increment ratio ($R_{k,i}$)	**Value**
$R_{1,i}$ = (Twin Lakes ponderosa pine)/(defoliated pine)	$AITLP_i/AIDP_i$
$R_{2,i}$ = (lava flow ponderosa pine)/(defoliated pine)	$AILFP_i/AIDP_i$
$R_{3,i}$ = (Twin Lakes ponderosa pine)/(sugar pine)	$AITLP_i/AISP_i$
$R_{4,i}$ = (lava flow ponderosa pine)/(sugar pine)	$AILFP_i/AISP_i$
$R_{5,i}$ = (sugar pine)/(defoliated pine)	$AISP_i/AIDP_i$
$R_{6,i}$ = (lava flow ponderosa pine/Twin Lakes ponderosa pine)	$AILFP_i/AITLP_i$

Step 2: For 1985-91 each of the six sets of ratios was related to year by using polynomial regression after transforming the years 1985 to 1991 to 1 through 7. The relation of the first four ratios and the transformed year values (TYV = i) was linear,

$$R_{k,i} = a_k + b_k(TYV) \ . \qquad (2)$$

Step 3: Values of $R_{1,i}$, $R_{2,i}$, $R_{3,i}$, and $R_{4,i}$ for 1992, 1993, and 1994 if defoliation had not occurred were estimated by using model (2) with intercept and slope values for 1985-91 and TYV or i values of 8, 9, and 10. These estimates rest on the assumption that model (2) would describe these ratios through 1994 without defoliation.

Step 4: Obviously,

$$AIDP_i = AITLP_i/(AITLP_i/AIDP_i) = AILFP_i/(AILFP_i/AIDP_i) \ .$$

Defoliation did not influence $AITLP_i$ or $AILFP_i$. A value of ($AITLP_i/AIDP_i$) or ($AILFP_i/AIDP_i$) without defoliation would allow prediction of $AIDP_i$ without defoliation. Model (2) provides a way to estimate ($AITLP_i/AIDP_i$) and ($AILFP_i/AIDP_i$) without defoliation for 1992, 1993, and 1994 (note step 3). Adjusted means for tree basal area increments of the Twin Lakes ponderosa pine ($AITLP_i$) for 1992, 1993, and 1994 were, therefore, divided by the ratios of $AITLP_i/AIDP_i$ estimated for 1992, 1993, and 1994 from model (2) in step 3 to predict adjusted means of basal area increments for ponderosa pine trees in the spacing study area without pandora moth. A second set of adjusted means for the same tree basal area increments for 1992, 1993, and 1994 was calculated by using the basal area increments of the lava flow ponderosa pine ($AILFP_i$) and ratios $AILFP_i/AIDP_i$ determined from model (2). For example, dividing the 1992 adjusted mean for $AITLP_8$ by the ratio $AITLP_8/AIDP_8$ for 1992, determined from model (2) in step 3, would predict a value for the annual increment of defoliated ponderosa pine for 1992 without defoliation ($AIDP1_8$):

$$AIDP1_8 = AITLP_8/(AITLP_8/AIDP_8) .$$

Similarly, a second set of values for AIDP in 1992 without defoliation ($AIDP2_8$) was predicted from lava flow ponderosa pine annual increments (AILFP) and the appropriate ratio $AILFP_8/AIDP_8$ estimated from model (2) in step 3:

$$AIDP2_8 = AILFP_8/(AILFP_8/AIDP_8) .$$

Two values for sugar pine annual increments without pandora moth ($AISP1_i$ and $AISP2_i$) also were predicted for 1992, 1993, and 1994 (i = 8, 9, 10):

$$AISP1_i = AITLP_i/(AITLP_i/AISP_i) ,$$

and,

$$AISP2_i = AILFP_i/(AILFP_i/AISP_i) ,$$

where ($AITLP_i/AISP_i$) and ($AILFP_i/AISP_i$) were estimated in step 3. The two estimates of predicted adjusted means of annual basal area increment without defoliation in the spacing study area for 1992, 1993, and 1994 determined from the Twin Lakes and lava flow adjusted annual increments and appropriate ratios from model (2) were averaged by species. These averages were used as the predicted adjusted mean of the annual basal area increment that would have occurred for 1992, 1993, and 1994 for the bored trees in the spacing study area without defoliation.

Results

Quadratic mean diameter (QMD) averaged 5.2 centimeters and average height was 3.6 meters for all treatments at the start of the spacing study (spring 1960). Thirty years later, when the recent pandora moth outbreak began, QMDs were 14.1, 17.4, 21.7, 26.9, and 30.7 centimeters for the narrowest to widest spacings, respectively, where understory vegetation was present. Corresponding average heights were 9.0, 9.5, 11.2, 12.9, and 13.7 meters. Corresponding basal areas were 37.5, 28.9, 22.4, 17.7, and 11.4 square meters/hectare. Corresponding volumes were 143.0, 111.4, 94.9, 82.3, and 54.7 cubic meters/hectare. For the narrowest to widest spacings without understory, QMDs averaged 14.6, 18.2, 23.9, 29.8, and 36.8 centimeters and heights averaged 9.0, 10.3, 12.4, 14.4, and 15.0 meters. Corresponding basal areas were 40.1, 32.0, 27.0, 21.5, and 16.3 square meters/hectare, and corresponding volumes were 152.4, 128.9, 123.2, 111.8, and 85.1 cubic meters/hectare.

Table 1—Probability of higher F-values in the split plot analysis of variance of defoliation in 1992 and 1994

Source	Df[a]	Probability of higher F-value
Whole plot:		
Spacing (space)—		
Linear	1	.0017
Quadratic	1	.0013
Cubic	1	.5972
Quartic	1	.8499
Understory (veg)	1	.9067
Space × veg	4	.3172
Error	20	
Split plot:		
Year (yr)	1	.0001
Yr × space—		
Linear	1	.1819
Quadratic	1	.1731
Cubic	1	.6592
Quartic	1	.5623
Yr × veg	1	.2627
Yr × space × veg	4	.2750
Error	20	
Error mean square:		
Whole plot		231.8833
Split plot		232.0500

[a] Df = degrees of freedom.

Plot Defoliation

Defoliation in 1992 averaged 44.5 percent (range 5 to 75 percent) of the 1991 and older needles for the spacing study plots. Defoliation in 1994 was significantly higher ($p \leq 0.10$), averaging 67 percent (range 45 to 85 percent) of the 1993 and older needles (table 1, fig. 1). Percentage of defoliation was curvilinearly related to spacing as indicated by the significance ($p \leq 0.10$) of the quadratic component of the spacing term in the analyses of variance (table 1). Percentage of defoliation generally increased as spacings increased from 2 to 5.7 meters and then decreased as spacings increased to 8 meters (fig. 1). Significant ($p \leq 0.10$) differences were not detected in curve shape for the percentage of defoliation-to-spacing relation in 1992 and 1994. No significant ($p \leq 0.10$) differences in defoliation occurred with understory treatment.

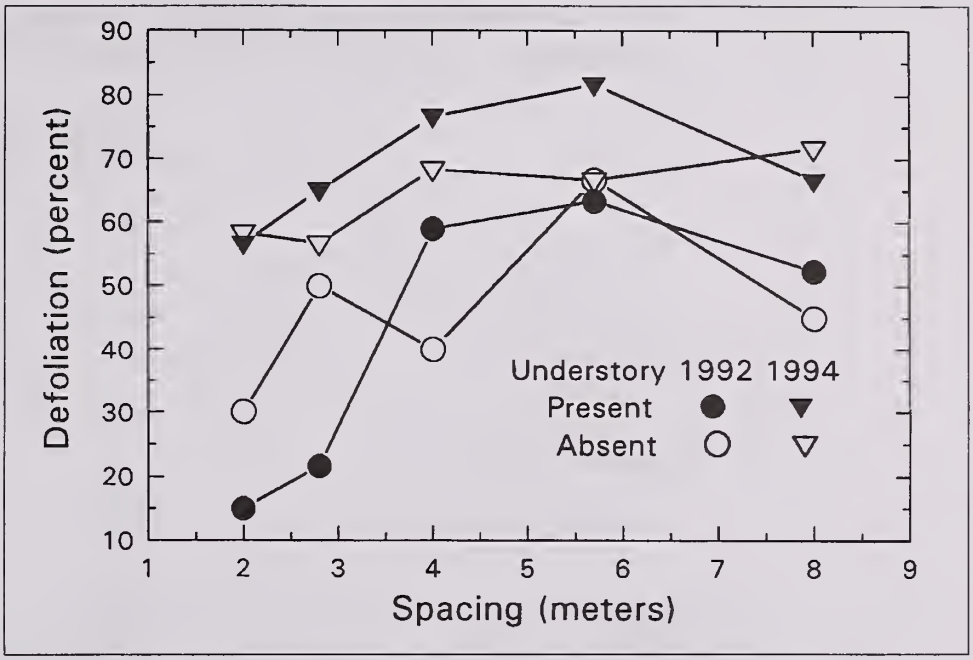

Figure 1—Percentage of defoliation in relation to spacing. Each point represents an average of three plots.

Ponderosa Mortality and Stand Growth

Only 9 of the 2,177 trees on the spacing study plots alive in the spring of 1990 died in 1990-94. No mortality occurred in two of the seven previous periods. Mortality in the other five periods before the pandora moth outbreak was the same or higher than 1990-94.

Percentage of height growth during 1990-94 was reduced ($p \leq 0.10$) by defoliation in 1994, and percentage of volume growth was reduced by defoliation in 1992 ($p \leq 0.10$) (table 2, fig. 2). A significant ($p \leq 0.10$) reduction in basal area growth for the spacing study due to defoliation was not detected. All percentages of growth rates were greatest ($p \leq 0.10$) where understory vegetation occurred. Percentage of volume growth generally increased ($p \leq 0.10$) with increased spacing (table 2, fig. 2), and percentage of height growth increased linearly ($p \leq 0.10$) with increased spacing. Results of the analysis of covariance model indicated that percentage of volume growth at the 2-meter spacing was reduced from 2.25 percent for no defoliation to 1.75 percent for the lightest defoliation, to 1.2 percent for the defoliation, to 0.7 percent for the highest defoliation (fig. 2). Percentage of volume growth at the widest spacing (8 meters) was reduced from 4.5 percent for no defoliation to 4 percent for the lightest defoliation, to 3.3 percent for average defoliation, to 2.8 percent for the highest defoliation.

Table 2—Probability of higher F-values in the analyses of covariance of growth percentages of basal area, height, and volume in the spacing study for 1990-94

Source	Df[a]	Probability of higher F-value		
		Basal area	Height	Volume
Regression (% growth vs % defoliation 1992)	1	0.1123	0.3337	0.0308
Regression (% growth vs % defoliation 1994)	1	.3717	.0153	.1125
Spacing (space):				
Linear	1	.5388	.0055	.0046
Quadratic	1	.7008	.3484	.5431
Cubic	1	.0014	.9113	.0227
Quartic	1	.9804	.3603	.9815
Understory (veg)	1	.0009	.0601	.0021
Space × veg	4	.2089	.1102	.2580
Error	18			
MSE[b]		.0241	.0631	.0932
C.V.%[c]		13.6	18.2	11.2

[a] Df = degrees of freedom.

[b] MSE is the mean square for error from the analyses of covariance.

[c] C.V.% is the coefficient of variation.

Individual Ponderosa Pine and Sugar Pine Trees

Averages for estimated diameters outside bark in spring 1985 were 19.3 centimeters for the 17 sugar pine in the spacing study area, 20.0 centimeters for the 23 partially defoliated ponderosa pine in the spacing study area, 19.3 centimeters for the 31 ponderosa pine near Twin Lakes, and 17.2 centimeters for the 23 ponderosa pine from the lava flow. Ponderosa pine in the spacing study area grew less in basal area since 1985 than the sugar pine in the spacing study area or the ponderosa pine in the other two areas (fig. 3). A large shift in basal area growth rates occurred in 1992 (fig. 3, tables 3 and 4) when partial defoliation of ponderosa pine in the spacing study area first occurred, resulting in a significant ($p \leq 0.10$) period-by-species-area interaction (table 3) for annual basal area increments of individual trees. In the spacing study area, sugar pine produced 1.5 times more basal area per tree than the ponderosa pine in the 3 years before ponderosa pine defoliation and four times as much basal area per tree in the 3 years after defoliation. Ponderosa pine at Twin Lakes produced 1.7 times more basal area per tree than ponderosa pine in the spacing study area in the 3 years before partial defoliation and four times as much basal area per tree in the 3 years after defoliation. Ponderosa pine from the lava flow produced 2.8 times more basal area per tree than ponderosa pine in the spacing study area in the 3 years before partial defoliation and 6.4 times as much basal area per tree in the 3 years after defoliation (table 4).

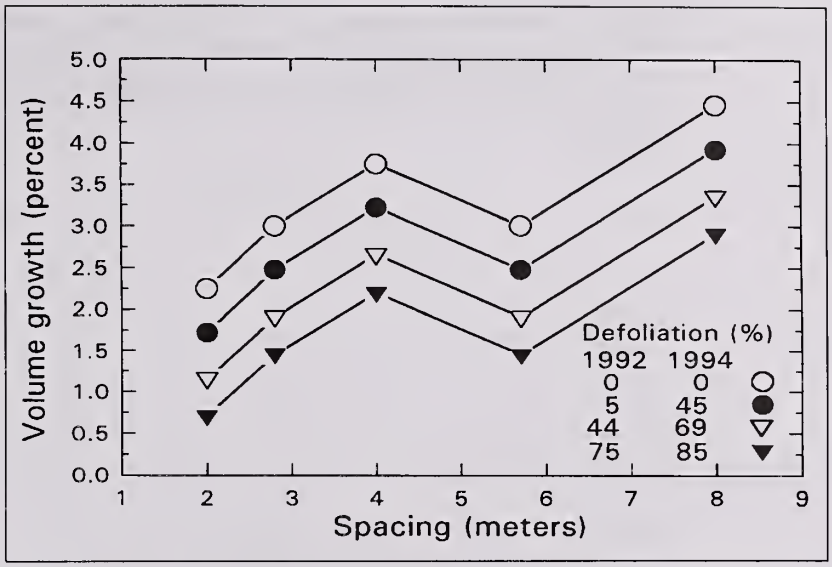

Figure 2—Predicted percentage of volume growth with understory vegetation for 1990-94 in relation to spacing and four levels of defoliation: none, the lowest defoliation rates (5 percent in 1992 and 45 percent in 1994), average defoliation rates (44 percent in 1992 and 69 percent in 1994), and the highest defoliation rates (75 percent in 1992 and 85 percent in 1994).

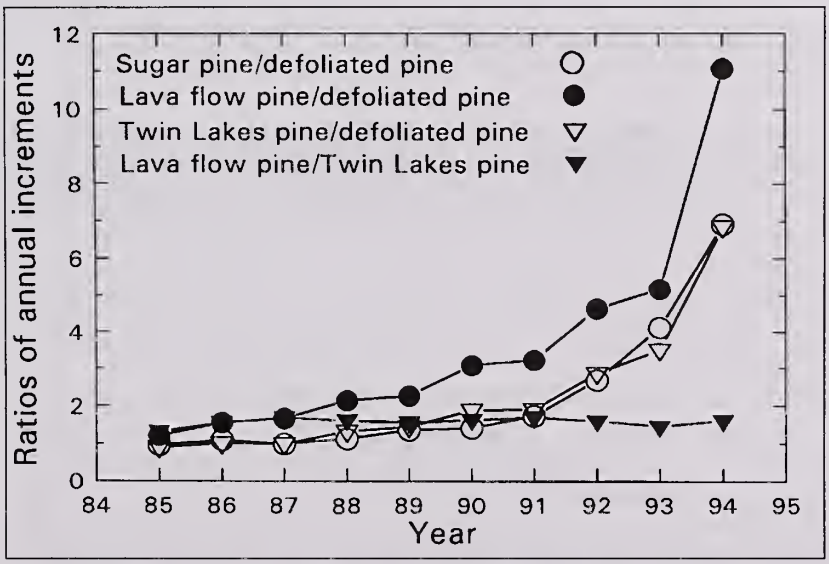

Figure 3—Ratios of adjusted means of annual basal area increments for seven growing seasons before the 1992 defoliation and three growing seasons afterward. Ratios were calculated from increments adjusted to a common basal area at the start of each growing season.

Table 3—Probability of higher F-values in the split-plot analyses of variance of basal area periodic annual increments of individual trees for the 4 species-area combinations 3 years before partial defoliation by pandora moth in the spacing study area (period 1; 1989-91) and 3 years after partial defoliation (period 2; 1992-94)

Source	Df [a]	Probability of higher F-values
Whole plot:		
Species-area (SA)	3	0.0001
Error	90	
Split plot:		
Period (P)	1	.0001
P × SA	3	.0001
Error	90	
Error mean square:		
Whole plot		.00000135
Split plot		.00000010

[a] Df = degrees of freedom.

Table 4—Average basal area periodic annual increments (PAIs) per tree for the 4 species-area combinations for 3 years before the pandora moth outbreak in the spacing study area (1989-91) and 3 years after the outbreak (1992-94)

	PAIs (cm^2/tree)	
Species-area	1989-91	1992-94
Ponderosa pine-spacing study area	10.7	4.3
Sugar pine-spacing study area	15.8	17.3
Ponderosa pine-Twin Lakes	18.4	17.0
Ponderosa pine-lava flow	30.2	27.5

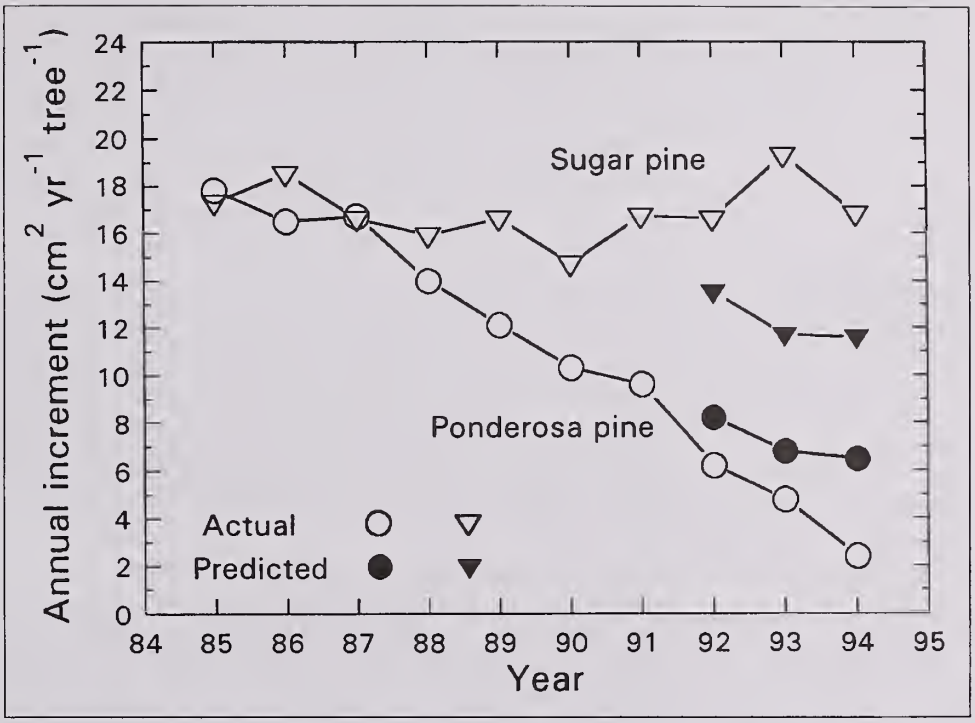

Figure 4—Actual adjusted means of annual basal increments for bored ponderosa pine and sugar pine in the spacing study area for 1985-94 and adjusted means for 1992-94, predicted without defoliation.

The r^2 values for ratios of annual basal area increments of Twin Lakes ponderosa pine/defoliated pine and lava flow ponderosa pine/defoliated pine fit for 1985-91 by using model (2) were 0.92 and 0.96, respectively. Predicted values for adjusted means of annual basal area increments for ponderosa pine in the spacing study area without defoliation, determined by dividing the adjusted means of the annual increments of the Twin Lakes ponderosa pine in 1992, 1993, and 1994 by ratios predicted from model (2) for these years, were 8.4 square centimeters/tree (1992), 7.3 square centimeters/tree (1993), and 6.7 square centimeters/tree (1994). Predicted values from the lava flow ponderosa pine data were 8.0 square centimeters/tree (1992), 6.3 square centimeters/tree (1993) and 6.3 square centimeters/tree (1994). Actual values were 6.2 square centimeters/tree (1992), 4.8 square centimeters/tree (1993), and 2.4 square centimeters/tree (1994) for the defoliated ponderosa pine (fig. 4). Reductions due to pandora moth were 27 percent (1992), 35 percent (1993), and 64 percent (1994) using Twin Lakes data and 23 percent (1992), 25 percent (1993), and 61 percent (1994) using lava flow data. Average reductions were 25 percent (1992), 30 percent (1993), and 62 percent (1994).

The r^2 values for ratios of annual basal area increments of Twin Lakes ponderosa pine/sugar pine and lava flow ponderosa pine/sugar pine fit for 1985-91 by using model (2) were 0.54 and 0.69, respectively. Predicted values for adjusted means of annual basal area increments for the sugar pine in the spacing study area, determined by dividing the adjusted means of the annual increments of the Twin Lakes ponderosa pine in 1992, 1993, and 1994 by ratios predicted from model (2) for these

years, were 14.0 square centimeters/tree (1992), 12.7 square centimeters/tree (1993), and 12.2 square centimeters/tree (1994). Predicted values from lava flow ponderosa pine data were 13.1 square centimeters/tree (1992), 10.7 square centimeters/tree (1993) and 11.1 square centimeters/tree (1994). Actual values were 16.6 square centimeters/tree (1992), 19.4 square centimeters/tree (1993), and 16.8 square centimeters/tree (1994) for the sugar pine (fig. 4). Average increases in sugar pine basal area growth coinciding with partial defoliation of ponderosa pine were 23 percent (1992), 65 percent (1993), and 44 percent (1994).

Discussion and Conclusions

Defoliation of the spacing study plot probably was influenced by the amount of foliage, moth oviposition behavior, and larval survival. Moths choose foliage for egg deposition first, if possible. If competition exists among female moths, eggs may be deposited on bark, understory vegetation, and even litter (Schmid and Bennett 1988). Possibly fewer eggs were deposited in the plots with 8-meter spacing, resulting in less defoliation. For the other spacings, decreased plot defoliation with decreased spacing simply may be the result of increased amounts of foliage being attacked by about the same number of larvae.

Predictions of percentage of growth for 1990-94 for the spacing study plots without defoliation were approximate because some defoliation occurred in all plots. The results, however, showed partial defoliation by pandora moth reduced ponderosa pine height and volume growth for 1992-94. Mortality for 1992-94 seemed to be unaffected by partial defoliation. The outbreak had not collapsed when the spacing study plots were last measured (fall 1994) and growth rates will continue to be lower for an unknown period. Before the outbreak, the trees had a 3- to 5-year needle complement. If full growth depends on a restored needle complement, growth will be low for 2 to 4 years after the end of the outbreak. Resumption of full growth may be sooner than 2 to 4 years, if larger needles are produced in postoutbreak growing seasons.

Estimates of growth changes due to defoliation for bored trees depend on the assumption of linear relations between the basal area increment ratios used and transformed year values through 1994 if defoliation had not occurred. This assumption seems reasonable considering the ratio that did not involve defoliation (lava flow ponderosa pine)/(Twin Lakes ponderosa pine). Unlike the other ratios, this ratio (fig. 3) was not related ($p \leq 0.10$) to TYV, indicating the relative basal area growth rates of the two sets of nondefoliated ponderosa pines did not change with time. This ratio also did not differ significantly ($p \leq 0.10$, statistics not shown) between 1985-91 and 1992-94, suggesting that the other ratios would have stayed on the same linear course without defoliation.

Predicted sugar pine annual basal area growth during 1992-94 was less certain than predicted ponderosa pine growth because of the lower r^2 values for the relation described by model (2). Lower predicted than actual values for sugar pine (fig. 4) were expected, however. More nutrients may have been cycled into the soil through frass produced by the larva (Miller and Wagner 1989). Reduced transpiration rates and perhaps reduced nutrient uptake by the partially defoliated ponderosa pine may have resulted in more water and nutrient uptake by the scattered sugar pine, further accentuating the differences in growth rates between the two species in 1992-94.

Patterson (1929) reported that increment loss due to pandora moth was "entirely dependent upon degree of defoliation," and he estimated that several years would pass before severely defoliated trees would regain their normal growth rate. Schmid and Bennett (1988) also found growth loss to be influenced by defoliation severity and frequency; a 25-percent reduction in basal area growth occurred in stands defoliated twice but no significant growth reduction occurred in stands defoliated once. In contrast, Miller and Wagner (1989) reported that "basal area growth is not directly proportionate to defoliation intensity" and that growth increased in heavily defoliated trees one year after the last defoliation. Results from the spacing study indicated that volume growth decreases with increasing defoliation. Results from individual tree sampling imply that defoliated tree growth rates in 1993, following the initial 1992 defoliation, were even lower than in 1992. The lack of a clearly significant relation between basal area growth and defoliation, and height growth and 1992 defoliation for the spacing study plots was probably due to uneven defoliation among trees in a given plot. In some cases, trees growing better before the outbreak may have been more or less severely defoliated than the plot average, thereby increasing the variability of the plot defoliation-plot growth relation. An individual tree modeling procedure would, in similar cases, produce a more accurate depiction of defoliation and stand growth.

Higher basal area and volume PAIs occurred without understory in early periods of the spacing study because of increased water, and perhaps nutrient, availability to the trees. This was not the case for the last four periods when PAIs were adjusted for plot basal area or volume at the beginning of each period. This difference in response to understory was caused by changes in soil quality that developed with time in the two understory conditions. Plots with understory had higher soil nitrogen (N), carbon (C), and higher microbial biomass C in the upper soil horizon than plots without understory by 1990-94 (Busse and others 1996). The higher soil quality and presumably higher foliar nutrient content in plots with understory did not clearly influence defoliation in the spacing study. Wickman and others (1996) found that fertilization of ponderosa pine plots in central Oregon, on a similar soil, during the current pandora moth outbreak with 350 kilograms N per hectare increased radial growth and foliar N concentrations. Surprisingly, they found larval weights in May 1990 were reduced in the fertilized plots, although no differences were found in pupal weights in September 1990. My results do not clarify the relation of soil quality, fertilization, and impact of pandora moth.

Schmid and Bennett (1988) reported that stand structure and tree size do not seem to influence oviposition behavior or larval survival, so silvicultural activities have little potential for suppressing outbreaks. Schmid and Bennett (1988) did, however, recommend silvicultural treatments that maintain desirable stocking levels and reduce the incidence of dwarf mistletoe (*Arceuthobium campylopodum* (Engelm.) Gill) to reduce growth and mortality losses in areas subject to pandora moth outbreaks. Proper stocking levels also are important to lower the probability of severe losses to bark beetles during the recovery period. Susceptibility of the partially defoliated and currently slow-growing trees in the spacing study area to mountain pine beetle (*Dendroctonus brevicomis* Lee.) and partially defoliated old-growth trees in the surrounding area to western pine beetle (*D. monticolae* Hopk.) may increase. Patterson (1929) reported serious outbreaks of these beetles in defoliated stands in south-central Oregon in 1923, 5 years after the beginning of a pandora moth outbreak. Mountain pine beetle populations were high in central Oregon before the current pandora moth outbreak began.

The ongoing drought has resulted in low stand growth rates in Oregon for some time, and defoliation by pandora moth has reduced growth even further. The effects of drought and defoliation are not yet over. Although the pandora moth outbreak has not increased tree mortality rates, serious mortality from bark beetles could occur in the next few years.

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